THE ROLE OF HOST-PLANT SELECTION
IN BEE SPECIATION PROCESSES

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Relatively large numbers of bee species are resident in the major floristic regions of North America (ca. 350-900; Moldenke, 1979). Many such broadly sympatric species are congeneric and directly compete for common resources or most probably are descended from ancestors which did compete before the presumed recent evolution of distinguishing non-competitive niche characteristics. Examination of sympatric congeneric species can suggest the axes along which such species have differentiated (if indeed they have), and comparative study can reveal which types of character displacement are likely to occur under similar conditions.

Analysis will be confined to relatively closely related congeneric bee species, because bees as a group are known to be highly variable in respect to such characteristics as nest location and substrate, predators and parasites, energetic requirements and periods of activity, and behavioral/morphological traits which permit the exploitation of particular resources. Since further physiological and nutritional characteristics quite probably also vary widely, confining analysis to closely related species can minimize differences and perhaps enable examination of the axes on which the speciation process(es) in bees operates.

Biological knowledge of the several thousand bees in North America is not extensive. Useful reviews, such as those of Linsley (1958) and Stephen et al (1969), as well as chapters associated with recent taxonomic treatments (e.g., Rozen (1958), Shinn (1967), Rust (1974), Thorp (1969) and Daly (1973)) serve to point out more of what is not known, than what in fact is established. The geographic distributions of most bee species are also known very imprecisely, information generally limited to imprecise broad geographic regions and perhaps an indication of the plant genus/genera with which it has been associated by collectors. Comprehensive faunal analyses of precise locations are largely limited to those of Robertson (1929), Pearson (1933), Moldenke (1971), Moldenke & Neff (1974) and Neff (unpub.). Quantification of the levels of

sympatry amongst sibling species in different regions and their degree of host-specialization/switching has not been attempted for the total pollen-collecting bee fauna of North America. This paper represents such an attempt, admittedly very preliminary in view of the data base, to isolate the relative emphasis placed upon host-specialization and host-switching in the speciation and competitive processes in bees.

A unique hypothesis of speciation in bees was presented by Linsley & MacSwain (1957), in an examination of the locally species-rich and highly sympatric genus Diadasia, which postulated the occurrence of sympatric speciation following intense local competition. Since the possibility of sympatric speciation in bees has been raised, there is the question of whether or not it occurs, and if so how often? If it were to occur, how would it be possible to recognize past instances thereof? First, one must recognize that any such sympatric speciation events that may have taken place in the past and have resulted during the course of time in allopatric species today, would probably be technically impossible to elucidate. Therefore, one must look for instances of species pairs or clusters which are largely or completely sympatric, from which one may infer that they are at least candidates for sympatric speciation events. This is not to say that any or all sympatric siblings necessaril result from a process of sympatric speciation, only that these species are the best candidates for future analysis to determine the mechanism(s) which function(s) as the usual isolating event.

In point of fact, it appears circumstantially that the majority of speciation in bees is in the traditional allopatric mode, since the overwhelming majority of closely related species clusters have primarily non-overlapping distributions. The occurrence of large numbers of congeneric bee species in a particular region (many of which have very distinctive behaviors or morpho-logical features associated with resource gathering) primarily represents independent colonization events or relative antiquity, since most of the distinctive species belong to distinct lineages which must have diverg a relatively long time ago, when the species in question (or the ancestors thereof) were quite probably living in very different geographic locations and were faced with competitive regimes no longer extant. This is not to imply, of course, that there are not narrow zones of overlap in regions of contiguous ranges of sibling species; such overlaps are to be expected and in the future should yield a great deal of information pertinent to the competition process. Most groups of bees are not well enough known, however, to permit this type of

analysis. Significantly, recent monographic treatment of _Ceratina_ (Daly, 1973) has noted strong character displacement of secondary sexual characters in regions of sympatry of closely-related primarily allopatric species.

Sympatric siblings occur in all regions of North America. However, in this present analysis only about 225 instances of sympatric closely related species were noted, in a total fauna of several thousand. The Halictinae, however, have not been included in this analysis since the genera remain unmonographed at this date; personal field work implies that many species are sympatric and pertinent in this context. Broad areas of sympatry between primarily Great Plains species and Eastern Deciduous Forest species in the area of the midwest were usually excluded from the citations below, because of the problem of geographic resolution of the data recorded on most distribution maps and the interdigitating nature of the major forest and grassland floristic elements in this region. My own personal observations of bees within the eastern United States convinces me that much of the present-day overlap in bee species there is due to the disturbance wrought by man and the concomitant wide and rapid spread of many species of plants and the pronounced opening up of the canopy between areas of rich melittophilous understory growth formerly quite isolated (relative to bee vagility).

In an extreme instance, _Xenoglossa strenua_ and _X. kansensis_ are now widely sympatric over much of North America following their presumably independent switches to the utilization of cultivated taxa of _Cucurbita_ from possible pre-colonial distributions centered in Mexico and the southern prairies respectively. Though many species of lacustrine plants may have been originally distributed throughout the northeastern United States (i.e., _Verbena hastata_), their recent history is clearly characterized by immense population increases and distributional expansion following logging and the introduction of cattle, providing incidently more stable and extensive nesting sites for Great Plains bees which have only recently (apparently) expanded eastwards in great numbers (i.e., _Calliopsis nebraskensis_; _V. hastata_ is heavily pollinated today by lepidopterans and many groups of polylectic bees and presumably did not necessitate the presence of this specialist-feeder prior to agricultural development of the Northeast and Midwest to successfully set outcrossed seed.)

METHODS:

        Published phylogenetic trees of North American bee
genera were utilized whenever available, without reinter-
pretation except in the instance of <u>Andrena</u> (<u>Micrandrena</u>
& <u>Scaphandrena</u>) as detailed in Moldenke (1979). Phylo-
genetic trees were prepared for many other bee genera in
coordination with the previously mentioned paper on host
choice. Some unmonographed genera (e.g., <u>Anthidium</u>,
<u>Hesperapis</u>, <u>Pterosarus</u>, <u>Dianthidium</u>, <u>Xenoglossodes</u>,
<u>Anthophora</u>, <u>Emphoropsis</u>, <u>Exomalopsis</u>, <u>Panurginus</u>, <u>Osmia</u>
(<u>Chenosmia</u>, <u>Monilosmia</u> & <u>Nothosmia</u>), <u>Andrena</u> (as of yet
unmonographed subgenera) and the Halictinae) were not
analyzed and are not treated in this paper. Distribu-
tional data from monographic treatments, Mitchell (1960,
1962), Meusebeck et al (1951), Moldenke & Neff (1974b)
and Neff (unpub.) was incorporated at the level of
broad floristic provinces inhabited and broad altitudinal
ranges. Floristic regions are the same as those utilized
in Moldenke (1979; e.g., Boreal Forest, Oak Hickory/
Mixed Mesophytic Forest, Oak Hickory Pine Forest, Southern
Mixed Forest, Great Plains, Great Basin, Rocky Mountains,
Pacific Northwest Forests, Mediterranean California and
southwestern Desert) with resolution of sympatry
generally to the scale of state within the eastern United
States or general elevational relief within the western
United States; actual associated plant community data is
available only in California (Moldenke & Neff, 1974b).
Point site occurrence data was not included since it is:
1) generally unavailable for nearly all parts of the
continent; 2) may be biased in overestimating the rich-
ness of sympatric taxa since it is temporally constrained
and may include ecotonal elements; and 3) may be biased
in underestimating co-occurring taxa due to sample error.
Hence the information tabulated in this report does not
attempt to make a complete accounting of sympatric
closely related taxa, but rather tries to analyze the
general nature of bee distributions and host-plant
utilization for only those bee groups which have been
monographed fairly recently.

        The use of the terms "sibling" or "closely-related
congeneric" species in this paper indicates only general
overall morphological similarity (often based on the
genital and associated structures in many bee groups)
and does not imply anything about ease of distinguishing
the species in terms of colorational or pubescence
characteristics. Closely-related groupings of such
"sibling species" usually contain from 1-6 (averaging
2-4) species, and are arbitrarily delimited on the basis
of the general structure of published cladograms and the
subjective similarity of character correlations and

genitalic illustrations of genera without published
phylogenetic accounts. A conscious effort is always
made to reduce the number of members of such groups to
a minimum to emphasize the distribution patterns of
presumably only the most closely related and biologically
most similar taxa in the hope of discovering as many
possible instances that might later be examined for the
possibility of sympatric speciation. More distantly
related congeneric or con-subgeneric taxa are treated
separately when instances of sympatry are high within
the genus/subgenus as a whole. Extremely rare taxa
about which little is known pertaining to host-selection
are usually excluded from analysis of possible modes of
diversification since they possess no reliable data.
Species or species-groups may (and often do) enter into
several of the tabular analyses if they demonstrate
divergence in more than one characteristic. Particular
examples cited in the results must not be interpreted as
proven instances of a particular character displacement;
data even for the relatively ecologically well-studied
bumblebees is not sufficiently robust, let alone for the
universally poorly-studied solitary bees. Such citations
are the most likely examples of particular trends based
on the data available to me presently.

RESULTS:
a) HOST-SWITCHING:

        Change of host-species pollen resource has always
been the aspect of bee/flower inter-relationships that
has intrigued me the most. An overall account of the
patterns of host change and specialization was presented
in Moldenke (1979). Many of the switches noted in the
phylogenetic illustrations of that paper are not included
below since such species which have split off ancestral
hosts are often deemed morphologically only distantly
related in many taxonomic treatments. They may, in
fact, be ancient splits in many cases, the results of the
types of gradual phenomena listed below. If, on the
other hand, speciation occurs in bees in much the same
manner as the rapid evolution seen in Drosophila (Carson)
and tephritid flies (Bush), then many such morphologi-
cally specialized oligoleges may in fact be much more
closely allied than usually treated in recent monographs.
The three major types of host switching phenomena
observed in sibling species involve the switch from
polylege to specialist (or generalist with heavy emphasis
on one genus only), switches between specialists upon
confamilial genera and the switch between taxonomically
unrelated host plants by specialist-feeding bees.

        The switch in host-choice among sympatric siblings

HOST-SHIFT CATEGORY	NUMBER SIBLING EXAMPLES	NUMBER NON-SIB EXAMPLES
POLYLEGE to **EMPHASIS or SPECIALIZATION**	23	7
$POLYLEGE_{emp\ 1}$ to $POLYLEGE_{emp\ 2}$	5	4
SPECIALIST $\longrightarrow$ SPEC. + POLY.	4	1
$GENUS_1$ to $GENUS_{2(confamiliar)}$	28	14
$SPECIES_1$ to $SPECIES_{2(congeneric)}$	6	1
$GENUS_1$ to $GENUS_{2(unrelated)}$	27	(many)

TABLE 1. CATEGORIES OF HOST SPECIALIZATION AMONGST SIBLING AND UNRELATED CONGENERIC/GENERIC SPECIES. Unrelated generic host-plant distinctions between non-sibs often meaningless to enumerate.

may involve a number of different forms. Most simply a polylege appears to give rise to a taxon which, though technically a polylege, is nearly always associated with one or two particular plant genera. Such is apparently the case with the species pair Hylaeus timberlakei (polylege) and H. calvus (emphasis Ceanothus/Eriodictyon) throughout the Sierra Nevada of California and Hoplitis producta producta (polylege) and H. producta bernardina (emphasis Penstemon) in the chaparral and forest understory of southern California. The change from polylege to specialist-feeder may be complete as in Ashmeadiella bigeloviae (polylege) and A. prosopidis (Prosopis specialist) throughout the southwestern deserts and may be accompanied by morphological specialization of the presumed derived species as in A. cactorum/A. bigeloviae (polyleges) and the small A. rufitarsis (Eriogonum oligolege) throughout much of mediterranean California. Alternately, the polylege may apparently adapt to a family-level specialist taxon or said family-level specialist may apparently become generically restricted; possible examples of the former are Melissodes thelypodii/M. gilensis (polyleges) and M. tepida (emphasis legumes) in the Sonoran Desert and Chelostomoides campanulae (polylege) with C. exilis et al.(emphasis legumes) throughout most of the eastern United States, the latter is abundantly represented by Chelostomoides chilopsidis (all tree legume genera) with C. discorhina (Cercidium +?) and C. odontostoma/C. browni?(Prosopis/

Acacia) throughout the southwestern deserts and
Melissodes confusa/M.elegans(composites in general)
with M. tincta (Aster/Chrysopsis) and M. coreopsidis
("sunflower genera") throughout the Great Plains which
again might be supplemented by considerable host-
related size divergence for example in M. agilis
(Helianthus specialist) relative to M. dentiventris
(Aster/Chrysopsis specialist) and the ancestors within
M. (Eumelissodes)(general composite feeders).

Another type of possible host-switch may be seen
best within the Perdita (Ventralis-subfasciata) group:
i.e., polylege(emphasis a)→polylege(emphasis b) [a
unrelated to b]. This group of more than 10 species
(inter-relationships unclear) is abundant throughout
the southwestern deserts; all the species are apparently
not truly generic-specialists, but generalists with
heavy facultative specialization. Species are strongly
sympatric and often active synchronously. The genera
facultatively specialized upon are as divergent as
Acacia, Washingtonia, Agave, Dasylirion and Nolina.
Within the reportedly polylectic Andrena species, A.
miranda (Rosaceae emphasis)/A. virginica (Ceanothus
emphasis), A. amphibola(not Ceanothus)/A. quintiliformis
(emphasis Ceanothus) and A. cyanopoda (Potentilla/
Ranunculus)/A. fuscicauda (Ceanothus) are potential
examples as well as Melissodes communis (emphasis
legumes and mints)/M. comptioides (emphasis composites).
Such host differentiation may entail an active host-
choice on the part of the bee, or might be an artifact
(as in case #3) of a change in habitat preference which
would automatically shift the preferred host as well.

Intriguing in this same vein are sibling pairs with
closely specialized feeding habits, one member of which
is implicated in exhibiting some minor degree of
polylecty: Andrena fragilis (Cornus +)/A. nigrifrons
(Cornus); Perdita larreae (Larrea)/P. marcialis (Larrea +);
P. maculosa et al. (Coldenia)/P. arenaria & P. rhodo-
gastra (Coldenia + Heliotropium); Andrena piperi
(crucifers)/A. scurra (crucifers + poly). Whether
these are examples of monophagic pollen-collecting
species which are merely poorly temporally synchronized
with their host and hence collected nectaring in greater
frequency, or they represent true polyphagous tendencies
in the light of some competitive pressure would be
fascinating to determine; the all too possible sample
bias might also obtain of course. The best estimate of
host-selection habits (short of scopal pollen analysis)
that I have found in my own research is the number of
separate collections of female bees with significantly
filled scopae; this data is seldom if ever available

outside of my own museum cataloguing in California.   Of
the three cited instances of sibling pairs of Andrena
with polylectic habits, but differing emphases, I
strongly suspect either sample bias or true allopatry
(inter-community or altitudinal) which is hidden by lack
of comprehensive knowledge of the species in question.
However, polylectic species of the Perdita (subfasciata
group) are clearly facultatively associated with different
plant genera locally though no individual species is a str:
oligolege; habitat preference may be the determining facto

    True generically unrelated host-switching among
sympatric closely-related bee species does indeed occur
rather frequently, occurring both between unrelated
plant species which are morphologically similar (Sidalcea
—→ Clarkia; Calochortus —→ Eschscholzia (i.e., Perdita)
as well as between completely unrelated and morphologi-
cally very dissimilar (nectar and scent chemistry?)
genera, e.g., Dalea —→ Larrea (Colletes); umbellifers —→
Trifolium and Ceanothus (Andrena); Arctostaphylos —→
Amsinckia (Synhalonia).   In nearly all of such generic
switches encountered, the original and recipient plants
are synchronous bloomers. The switch in Andrena between
Polemonium (A. segregans, A. ribblei?) and Ranunculus
(A. caerulea, A. suavis) involves a distinct time shift
as well.

    Where the individual sibling species have been
ecologically studied as well, a switch between different
congeneric host-plant species is encountered.   Andrena
chalybaea (Camissonia ovata specialist)/A. parachalybaea
(C. bistorta & C. cheiranthifolia) along the immediate
coast of southern California and A. eothina (C. campestris
A. anatolis (C. bistorta) throughout cismontane southern
California are well-documented examples, the latter
accompanied by a change in size and timing of daily
activity patterns as well.   The distinction between the
closely related Anthocopa (Eremosmia) and A. (Isosmia)
respectively specialized on tree and annual species of
Dalea is also associated with a marked shift in blooming
season as well in the southwestern deserts.   In the
Colorado Desert of California, Perdita clypeata (Eriogonum
inflatum specialist), P. distans (E. reniflorum), P.
nasuta (E. trichopes) and several other rare sympatric
species on specifically undetermined Eriogonum spp. may
possibly be shown at some later date to have a complex
group of species-specific (±) obligate host-restrictions.
Host-restriction by a bee species may be correlated to
the plant breeding system as seen in the large Chelostoma
phaceliae & C. incisulum which frequent many species of
large-flowered outcrossing Phacelia in cismontane
southern California, while C. minutum is restricted to
the tiny-flowered inbreeding P. davidsoni.

Examples of clearly established switches between confamilial genera are especially numerous within the Compositae (17 examples within Andrena, Melissodes, Perdita and Calliopsis) although they occur as well within the Leguminosae (i.e., Chelostomopsis), Loasaceae (i.e., Perdita), Cactaceae (i.e., Lithurgus), Malvaceae (i.e., Diadasia) and Hydrophyllaceae (e.g., Chelostoma, Dufourea, Protodufourea, Conanthalictus and Nomadopsis). Such switches are often accompanied by overall size changes, as well as seasonal activity phase shifts (at times pronounced as in Lithurgus apicalis et al. (on spring blooming Opuntia) to L. echinocacti (summer-blooming barrel cacti). This category of host-switching between different genera by sympatric siblings will undoubtedly increase greatly upon increased collection and research on the composite-feeders of the plains and deserts.

Distinctive coordinated temporal and host switches between somewhat related plant genera is often observed, i.e., the switch from Camissonia to Gayophytum (Dufourea and Andrena) and many of the intra-Compositae shifts. Though such examples involve plant genera which are presently characterized by distinctly non-synchronous blooming periods, paleohistorically such plants may have once bloomed synchronously (perhaps during the period of the bee host-switching). Since in fact, most temporal shifts are between confamilial genera and not between unrelated taxa, such a possibility seems highly likely. Not surprisingly a large percentage of these examples are from mediterranean California and desert Arizona, where the bee fauna has been studied in much more detail with respect to host-plant association and the distinct winter rainy period is paleohistorically very novel.

Differential host restriction also occurs between congeneric distantly-related sympatric bee species, but it is much more difficult to distinguish meaningful specific examples without more complete data on distribution and host choice. The distinction between polylege and either composite- or legume-specialist exists in Melissodes/Andrena and Ancylandrena respectively. Unrelated con-subgeneric/congeneric sympatric polyleges emphasizing different plants are undoubtedly more frequent than represented in Table 1, with the paucity of information available for the genera Andrena and Colletes in the eastern United States. However, several examples are available from the western United States: 1) A. (Tylandrena) subtilis (Ranunculus emphasis)/A. (T.) perplexa (Prunus+ emphasis) in montane western U.S.A.;

2) <u>Dufourea</u> <u>rhamni</u> (emphasis <u>Dendromecon</u>)/<u>D</u>. <u>scintilla</u> (emphasis <u>Camissonia</u>)/<u>D</u>. <u>sandhouseae</u> (emphasis <u>Eschsch-olzia</u>) in most mediterranean California (P. Lincoln, ms.); 3) <u>Melissodes</u> <u>tessellata</u> (emphasis Compositae)/<u>M</u>. <u>tepida</u> <u>timberlakei</u> & <u>M</u>. <u>communis</u> <u>alopex</u> (emphasis non-composites) through mediterranean California; 4) <u>Andrena</u> (<u>Euandrena</u>) <u>nigrihirta</u> (<u>Dentaria</u> emphasis); <u>A</u>. (<u>E</u>.) <u>nigrocaerulea</u> (emphasis <u>Linanthus</u>); <u>A</u>. (<u>E</u>.) <u>auricoma</u> (emphasis <u>Potentilla</u> & <u>Scrophularia</u>); <u>A</u>. (<u>E</u>.) <u>chlorura</u> (emphasis <u>Ceanothus</u> & <u>Arctostaphylos</u>) throughout montane western United States. The fourth example is particularly interesting, since the floral data (cited from my own site-specific results) indicates localized strong specialization tendencies, but more importantly a very strong habitat separation in California (respectively deep forest, grassland, woodland/savanna, chaparral); distinctions of closely-related broadly sympatric species along this type of distribution gradient is probably highly likely, but resolution not possible in general in light of the distributional data available for most bees (see analysis of <u>Ceratina</u> distribution by Daly (1973)).

The most abundantly documented form of displacement amongst unrelated congeneric species involves differ-ential specialization upon confamiliar plant genera. Examples abound in <u>Andrena</u> (<u>Callandrena</u>)(see Moldenke, 1979), <u>Perdita</u> and <u>Melissodes</u> within composite feeders, and are also represented by <u>Perdita</u> <u>vittata</u> <u>tricolor</u> (on <u>Wislizenia</u>/<u>Cleome</u>) versus <u>P</u>. <u>cleomellae</u>/<u>P</u>. <u>thelypodii</u>/<u>P</u>. <u>basinicola</u> (on <u>Cleomella</u>/<u>Thelypodium</u>) in the montane desert and Owens Valley of California; and <u>A</u>. (<u>Micrandrena</u>) <u>melanochroa</u> (<u>Fragaria</u>) versus <u>A</u>. (<u>Derandrena</u>?) <u>ziziaeformis</u> (<u>Potentilla</u>/<u>Waldsteinia</u>) throughout the Eastern Deciduous Forests. Differentiation on the species level occurs in <u>A</u>. (<u>Diandrena</u>) among <u>Camissonia</u> species, and <u>Perdita</u> among <u>Dalea</u> species; in both of these instances slight differences in habitat selection (altitude or community type) are suspected as well.

b) <u>CHANGING ENERGETIC BUDGETS</u>:

In this examination of sympatric sibling species, I have attempted to discover significant changes in body size that have occurred. This is not an original idea on my part (viz. Hutchinson, Schoener, Inouye, Brian, Dressler), but rather reflects my assumption that an analogous principle of limiting similarity must exist amongst pollen-gleaning bees as it does amongst guilds of vertebrate foragers. Whereas it is intuitively obvious how such a principle has validity where, i.e. the beaks of large birds can be correlated with efficiency in utilizing seeds of a particular size range, it is not so

obvious how such size differences could be correlated
with the differential utilization of precisely the same
floral resources. Though I do not know what the rela-
vant size range differential would have to be to achieve
significance, it certainly is exceeded frequently amongst
species of different genera working the same plant
resource.

The notion of limiting similarity has to be
approached from the point of view of environmental
grain. Rapidly depleting pollen and nectar sources in
flowers represent vastly different states of "graininess"
(sensu Levins) relative to bees' physiological costs of
harvesting it (especially with changing diurnal thermal
regimes). For instance, larger-bodied bees are often
capable of considerable heterothermy enabling activity
at ambient temperatures at which their smaller non-
heterothermic competitors are at a disadvantage (Neff
et al., 1977). However, this strategy, in order to be
successful, must utilize only concentrated resources,
since the strategy requires more resources to operate
the endogenous heat production and to nourish larger
baby bees. Hence there comes, of necessity, a point
of diminishing return in the gradual daily depletion
of resources (or the varying density of plant popu-
lations) at which the energetically less costly
strategies usually employed by smaller sympatric
species gain an insuperable advantage in gleaning
partially-depleted pollen resources from flowers.

Such a difference in the energetics of foraging
need not be automatically associated with body size;
Rust (1974) in his recent treatment of Osmia (s. str.)
has noted the strong difference in flight speeds and
behavior exhibited by the more-or-less equal-sized
synchronous sympatric polyleges, O. ribifloris and O.
lignaria, which are frequently observed in competition
at precisely the same locations on the same plant
species. Since, however, little is known about the
flight speeds of related bee species in general, I
have made special note in Table 2 only of rather large
differences in relative body size as revealed in
monographic treatments. Such measurements are seldom
geared to local populations but represent average
sizes over vast numbers of populations, hence this list
cannot be considered more than an abbreviated attempt
to pinpoint some of the more noticeable differences.

Table 2 contrasts with Table 1 in the abundance of
polyleges and oligolectic specialists upon the Compositae
(>50%). The most reasonable assumption is that species
which are normally exposed to a very wide range of

resource sizes and morphologies adapt most quickly by
altering their overall body sizes (perhaps with undetec-
ted differences in host choice emphasis as well),
whereas obligate specialist-feeding species have less
exposure to such differing resource states and hence
must differentiate most readily along other axes,
because (with the exception of Chelostoma on Phacelia
cited above) the plant genera cited in Table 2 do not
differ radically in floral size of relevant species.
In two clear cases, the change in size may also be
correlated to a shift in altitude (i.e., Hylaeus
basalis/H. nunnenmacheri; Dufourea spilura/D. subdavid-
soni), however in this sample, size is not correlated
with elevation. On the other hand, the larger Colletes
stepheni, is active in the very early morning and early
night, whereas its smaller siblings C. salicola, C.
covilleae and C. clypeonitens are active at Larrea
during the warm desert day (Hurd & Linsley, 1975).

    Size differentiation is much more frequent even
than shown in Table 2 amongst sympatric unrelated
congeners, rather than amongst siblings. This is because
only con-subgeneric species were considered in erecting
the table and the Bombinae and Halictinae are not
adequately represented; within most large bee genera
with several subgenera, size differentiation amongst
sympatric species utilizing the same resource is
commonplace. Such size/energetic displacement is charac-
teristic amongst the pollinators of most plant species
when the total range of local pollinators are considered,
i.e. the probable graded energetic requirements of
Phacelia pollinators in southern California -- Anthophora/
Synhalonia; Bombus; Pseudomasaris (specialist pollen-
collecting wasps); Anthidium; Colletes/Andrena/Osmia;
Evylaeus/Lasioglossum; Anthocopa/Ashmeadiella/Dufourea/
Osmia; Panurginus/Nomadopsis; Dialictus; Conanthalictus;
Perdita. Accurate quantification of limiting similarity
has not been attempted as of yet on a localized basis.

c) CHANGING TEMPORAL ACTIVITY PATTERNS:

    Many bee species are characterized by very short
adult life spans, often less than one month for a
particular species in a particular locality -- and
probably often only half that period for individual
pollen-collecting females. With short life spans
typical of many bees it is to be expected that closely

TABLE 2. SIZE DIFFERENTIATION IN SYMPATRIC SIBLING SPECIES AN
SYMPATRIC UNRELATED CON-SUBGENERIC SPECIES AS RELATED TO HOST
SPECIALIZATION.

sibling species

GENUS	NUMBER INSTANCES	SIZE DIFFERENTIATION
HYLAEUS	1	-- polyleges
COLLETES	2	-- Larrea, Mertensia
ANDRENA	8	-- Solidago/Aster, polyleges, Compositae, Cornus, Salix, Camissonia
PERDITA	9	-- Mentzelia, Eriogonum, Compositae, Coldenia
CALLIOPSIS	1	-- Euphorbia
ANTHOCOPA	1	-- Penstemon
CHELOSTOMA	1	-- Phacelia
HOPLITIS	1	-- polyleges
PROTERIADES	1	-- Cryptantha
OSMIA	1	-- Compositae
MEGACHILE	1	-- Compositae
SYNHALONIA	1	-- polyleges (emphasis legumes?)
MELISSODES	3	-- polyleges, Compositae
DUFOUREA	1	-- Gayophytum

non-sibling species

GENUS	NUMBER INSTANCES	SIZE DIFFERENTIATION
HYLAEUS	2	-- polyleges
ANDRENA	14	-- Helianthus, Camissonia, Aster/Solidago, Lepidium, Potentilla/Fragaria, Ceanothus, polyleges
PERDITA	7	-- Opuntia, Malacothrix, Eriogonum, Sphaeralcea, Tidestromia, Larrea
MEGACHILE	2	-- polyleges, Compositae
MELISSODES	3	-- Compositae
PSEUDOPANURGUS	1	-- Compositae
NOMADOPSIS	2	-- Eriodictyon, Trifolium
SVASTRA	2	-- Compositae
XYLOCOPA	2	-- polyleges
CERATINA	2	-- polyleges
BOMBUS	many	-- polyleges

TABLE 2.

I ENTIRE SEASON ACTIVITY versus DEFINED SUBSET

    Sibling species - 3   Non-sibling species - 3

II DIFFERENT ACTIVITY PHASES DURING BLOOMING SEASON

    Sibling species - 22 Non-sibling species - 6

1) Eriogonum in Colorado Desert
   sibling Perdita species
P. semilutea - xerophila - clypeata - nasuta
            distans
            labrata
   April   May   May-June   June-July
           -------thermophila-----------------
             May-October

2) Prosopis in southwestern deserts
   sibling Perdita species *
g. genalis - s. stathamae - p. flava
nigronotata   p. sulphurea   p. punctosignata
               discors
  Early   Mid   Late

   sibling Perdita species *
duplicata - a. ashmeadi - exclamans
       a. vierecki   difficilis
       nigricornis
       l. luciae
  Early   Mid   Late

3) Sphaeralcea in southwestern deserts
   Diadasia spp.
   lutzi   - diminuta   - megamorpha
   martialis   tuberculifrons olivacea
   palmarum   sphaeralcearum sphaeralcearum
   vallicola
   Early   Mid   Late

III DIFFERENT PHASES WITHIN DIURNAL PERIOD

    Sibling species - 3   Non-sibling species - 2

TABLE 3. DIFFERENTIATION IN TIME OF ACTIVITY

* Unpublished studies by Neff in Arizona may indicate that
this apparent temporal disjunction is artifactual and based
upon biased general collection data (Neff, pers. com.).

related sympatric species might be able to allocate
resources allochronically. Theoretically such diver-
gence could occur in two very different manners.
Firstly, polyvoltine or long-lived species active for
much of the year, could become univoltine for just a
specific synchronous portion thereof. Secondly, two or
more short-lived asynchronous species might be able to
partition the blooming period of the appropriate
resource.

     Examples of polyvoltine species of the
first type I have not encountered often in the litera-
ture, probably for the simple fact that in the temperate
United States few bee species are indeed active for
most of the possible flight season. Such species are
usually the social polyleges and the most diverse group
of the polyleges, the Halictinae, remains very incom-
pletely known and largely unmonographed. Six examples
are however cited in Table 3, two of which are polylectic,
two of which are Compositae-feeders and two of which
visit desert plant genera (i.e., _Larrea_, _Physalis_) which
facultatively respond to minimal desert water availabil-
ity and may be found (presently, at least, with agri-
culture, etc.) in bloom at nearly any time of year.
Hylaeus calvus has a very short flight season for
members of its genus, most species (i.e., its sympatric
sibling _H. timberlakei_) are active nearly throughout
the entire community blooming season. As with
temporally-delimited _H. sejunctus_ (emphasis _Prosopis_)
and its relatively-unrelated congeners, some degree of
host specialization is suspected. The Compositae-
feeding species of _Colletes_, _C. fulgidus_ (all year),
C. simulans & _C. angelicus_ (late summer/fall), are
very abundant sympatric sibling species, and though
there are occasional individuals of _C. simulans_ and
C. angelicus known from extremely early spring, the
temporal disjunction may be regarded as firmly estab-
lished. The examples of _Perdita binotata_ (fall)/ _P.
rozeni_ (spring) versus _P. physalidis_ (all year) on
Physalis and _Calliopsis timberlakei_/_C. pectidis_ versus
P. rozeni (all year) on Compositae are rare taxa which
might subsequently prove to be due to sample bias in
present collections. _Perdita larreae_ (summer bloom)
is abundant enough to assume true temporal differen-
tiation on _Larrea_ from _P. covilleae_ (spring bloom)
(Hurd & Linsley, 1975).

     The second type of temporal phase shift (i.e.,
non-synchronous short-lived specialists) is much more
frequent and I fully expect that future synecological
studies will discover a great many more examples, perhaps
on a localized population rather than a species-specific
basis. It is a most apparent phenomenon where whole

groups of congeneric species utilizing the same
specialized plant resource are sympatric (i.e., Perdita
on Prosopis; Perdita on Eriogonum; Diadasia on
Sphaeralcea). I am confident that the same temporal
shifts will be encountered when dominant composite
genera are examined in more detail (e.g., Haplopappus/
Chrysothamnus and Helianthus).

A particular form of phase shift occurs in regions
bordering upon mediterranean-type climates. As
Compositae are major elements of both the spring and
summer floras in these regions, shifts from autumnal/
summer activity to vernal activity (and occasionally
vice-versa) are possible. Such switches have not been
infrequent, and were noted on the phyletic lineages
presented in Moldenke (1979). Analogous shifts are
possible in the Sonoran Desert on genera of families,
other than the Compositae, which bloom during disjunct
desert rainy seasons (e.g., Sphaeralcea, Larrea, and
Cactaceae). Circumstantial evidence indicates that many
species may be primarily spring-active in California
deserts but summer-active in the vicinity of Tucson.
Since collecting in southcentral Arizona is not as
extensive as it is in desert California, such indications
may yet be proven artifactual. Type II changes are
especially frequent amongst bee groups associated with
the Compositae, comprising 50% or more of the examples
in both the sibling and non-sibling categories in Table 3.
Since the Compositae as a group are generally quite
diverse in most North American communities, individuals
of some species are generally in bloom for the entire
community anthesis period, thus facilitating the possi-
bility of such shifts. Examples of this phenomenon are
bound to increase as Compositae-feeders become better
known in the Great Plains and the southwestern deserts.

A third type of temporal shift is probably the
most common in practice, for theoretically it is probably
the most easily accomplished (and most difficult to
detect with the present data) -- namely, differing times
of activity during the diurnal cycle. Though seldom
looked for, and perhaps to be expected more frequently
between species of different genera utilizing the same
host resource, it has been documented by Thorp (1969) in
his revision of Andrena (Diandrena) associated obli-
gately with species of Camissonia, by Linsley et al.
(1963, 1964) with Andrena (Onagandrena) associated with
Camissonia and Hurd & Linsley (1975) with Larrea
specialists (also observed in Dufourea specialists on
Camissonia (Lincoln & Moldenke, ms)).

d) <u>CHANGING</u> <u>UTILIZATION</u> <u>STRATEGIES</u>:

The elegant paper of Hubbell & Johnson (1978) has demonstrated clearly that both closely-related congeners as well as unrelated congeners are able to coexist sympatrically by utilizing different types of exploitation strategies. Analogous differences in solitary- versus group-foraging, relative social aggressiveness and pheromonal food-territory marking are unlikely amongst most sympatric congeneric Canadian and United States bees; however, somewhat similar phenomena doubtless are operant to some degree amongst <u>Bombus</u> and halictine species. The wide range of social behavior exhibited amongst <u>Dialictus</u> from solitary to truly social bees may possibly be reflected in distinctive utilization strategies as well, but field confirmation is lacking as yet. Within <u>Bombus</u>, the ability of <u>Bombus</u> <u>terricola</u> to "rob" flowers with deep corolla tubes might be viewed as an adaptation permitting coexistence with similar-sized <u>Bombus</u> species which are able to utilize partially the same resources by means of longer tongues/faces, but in the more general view it is probably a competitive strategy against hummingbirds and sphinx moths and largely unrelated to sympatric bumblebee species.

e) <u>EQUIVALENT</u>(?) <u>SIBLINGS</u> and the <u>NATURE OF POLYLECTY</u>:

Table 4 indicates the richness of sympatric sibling and non-sibling species groups which a literature search has uncovered and which do not seem to differ conclusively in any set of noticeable as yet discovered characteristics. Species clusters oligolectic for the Compositae are especially prominent (21% siblings; 33% non-siblings respectively). The same genera of plants are associated with both siblings and non-siblings to a large extent, implying that groups mentioned in both portions of Table 4 have long demonstrated their particular host-selection strategies and that sibling sympatry has perhaps characterized these particular groups throughout their history.

Significantly, perhaps, the only host associations listed in Table 4 centered in the eastern half of the continent are polyleges, Compositae-feeders, Salix-feeders (i.e., <u>Parandrena</u>) and Cornus-feeders (i.e., <u>Gonandrena</u>). The pronounced altitudinal and rain shadow gradients in the western United States have clearly worked to produce more parallelly evolving anciently diverged clusters of species which remain conservative in their host-choices. That those bees should be associated with the arid regions which have

SIBLING SPECIES

POLYLECTIC	43	+halictines!
COMPOSITES	23	many
LEGUMES (DALEA)	10	many
SALIX	6	Andrena
SPHAERALCEA	4	Diadasia
LARREA	3	Colletes, Hesperapis, Nomadopsis
ERIASTRUM	2	Hesperapis, Perdita
PLATYSTEMON	2	Andrena
CRYPTANTHA	2	Proteriades
PHACELIA	2	Proteriades
PENSTEMON	2	Anthocopa
CUCURBITA	2	Peponapis, Xenoglossa
PYRRHOPAPPUS	1	Andrena
LASTHENIA	1	Andrena
EUPHORBIA	1	Calliopsis
PROSOPIS	1	Colletes
STEIRONEMA	1	Macropis
RANUNCULUS	1	Andrena
ARCTOSTAPHYLOS	1	Andrena
CLARKIA	1	Megachile
CACTACEAE	1	Diadasia
MALACOTHAMNUS	1	Diadasia

NON SIBLING SPECIES

POLYLECTIC	24	+halictines!
COMPOSITAE	23	many
SALIX	3	Andrena
CRUCIFERS	2	Andrena
DALEA	2	Perdita, Anthocopa
TREE LEGUMES	2	Ashmeadiella, Chelostomoides
AGOSERIS	1	Andrena
LUPINUS, LOTUS, ASTRAGALUS	1	Osmia
PETALOSTEMON	1	Colletes
LEPIDIUM	1	Perdita
LESQUERELLA	1	Andrena
PHYSALIS	1	Perdita
ERIASTRUM	1	Perdita
ESCHSCHOLZIA	1	Perdita
ERIOGONUM	1	Perdita
EUPHORBIA	1	Calliopsis
SPHAERALCEA	1	Diadasia
CUCURBITA	1	Peponapis
CORNUS	1	Andrena
CACTACEAE	1	Perdita
COLDENIA	1	Perdita
CALOCHORTUS	1	Perdita
PROSOPIS	1	Perdita
CLEOME	1	Perdita
PENSTEMON	1	Anthocopa
CRYPTANTHA	1	Proteriades
PHACELIA+	1	Anthocopa

TABLE 4. APPARENTLY EQUIVALENT SYMPATRIC SPECIES CLUSTERS.
Known examples of partial differentiation of 1 or 2 species
within a group along 1 or 2 different axes are included if
the differentiation is not sufficient to separate species
within the cluster as a whole.

repeatedly been the most dramatically effected (i.e., restricted to isolated regions) by climatic changes during the Pleistocene is surely not merely coincidental.

The most striking feature about species cited in this Table is the preponderance of polylectic-feeding bees (39% siblings; 33% non-siblings). "Polylectic" is a term which can, and is, used to cover a wide variety of feeding choice phenomena. In the sense I am using it, it means that the species is suspected of using a wide variety of taxonomically unrelated plant species for pollen sources throughout its distribution, though this might also be true at any one particular population throughout the course of the year. This does not imply that pollen sources are treated equivalently and that distinct host preferences might indeed be found for any particular time in any one population. Heinrich's extensive theoretical and field research, as well as that of Brown (1978), on bumblebees has shown this to be the predicted result of optimized foraging by bees with short memories and comparison-shopping behaviors. It is possible, that many non-_Bombus_ polyleges are behaviorly host-specialized to a large degree on different hosts in different parts of their distribution, however, the data available in the literature seldom permits this degree of accuracy except in certain specific instances.

For instance, studies on the agriculturally important _Megachile rotundata_ by Stephen & Torchio (1961) have shown that distinct populations do tend to specialize on unrelated host-plants in different parts of their range; indeed, on the Stanford University campus during the course of my pollination studies (1968-1970) both sexes of this species were found in enormous abundance on the introduced _Lotus corniculatus_, with individuals observed only infrequently on any other plant species in this plant species-rich region (garden plants, weeds and native chaparral).

Another case in point, the presumed polylectic wide-ranging (nearly throughout the non-desert United States) species, _Colletes kincaidii_ (and its ± allopatric sibling _C. eulophi_), is known to be closely associated with the fagaceous species _Lithocarpus densiflorus_ throughout Santa Cruz County, California (several dozen populations -- personal obs.) for both pollen and "nectar", which is apparently mostly fog condensation but contains detectable amounts of dissolved sugars. Females will visit _Adenostoma_, _Eriodictyon_ and _Rhamnus_ for nectar only, prior to the trees' anthesis. It is unknown what pollinates this

tree in the other parts of its range or whether C. kincaidii is ever associated with it elsewhere, however the bee must normally go to different sources since its range in California alone greatly exceeds that of tan-oak.

It is not known whether the majority of polylectic feeding patterns resemble the rather facultative type exhibited by M. rotundata or the less locally plastic type observed in C. kincaidii, presumably the former. If "polylectic" species do indeed facultatively specialize in local populations, then the opportunity exists for a large number of sympatric sibling polylectic species to avoid competition for food sources. If such food choices become heritable or conditioned (i.e., adult bee searches primarily for food with chemical characteristics it experienced as a larva) then such local assemblages could presumably remain quite stable assuming that plant abundances did not change drastically.

Such notions of food choice determinants for polylectic bee species merge indistinguishably with the known oligolectic patterns of feeders on various species of Compositae. Table 4 reveals that 20% of the sympatric species pairs for which no clear behavioral differences are known are obligately associated with the Compositae as pollen sources. Furthermore, most groups of Compositae-feeding bee species are heavily sympatric when the bee genus as a whole (and not just sibling species) is considered (e.g., Melissodes (Eumelissodes), Perdita (Cockerellia, Hexaperdita, Pentaperdita), Andrena (Callandrena, Cnemidandrena), Megachile (Sayapis), Calliopsis (Calliopsima), Pseudo-panurgus (s. str.)). The literature frequently records component species in long series from different composite species in different locations (even though apparently only one is utilized at any one site). Collection data is horrendously biased in these instances, of course, but the distinct probability exists that such "oligolectic" composite-feeders are indeed: 1) behaviorly generically specialized (and perhaps to some extent temporally and morphologically) in any one population; and 2) that this degree of specialization may indeed yield opportunities for considerably expanded local species richness phenomena.

Speciation rates in bees, on the obverse argu-ment, are apparently either fastest or most successful when component lineages have associated themselves with the multiple options open to specialists "on the family level" (such as composites; or legumes, e.g.,

Ashmeadiella, Colletes, Osmia -- an additional 10% on
Table 4) rather than specialists on non-diverse plant
groups (e.g., Proboscidea, Passiflora, Mentzelia,
Menodora) even if widely distributed (e.g., Lysimachia,
Oenothera s. str., Ipomoea, Heuchera, Gerardia, Larrea,
Campanula, Verbena, Lesquerella). The largest number of
bee species in each one of the genera cited above are
associated with the Compositae, far in excess of any
phyletic lineages associated with different plant groups;
the two other species-rich North American bee genera
with predominantly specialist-feeders, Colletes and
Osmia, both show major emphases on Compositae and
Leguminosae, and indeed the genus Megachile contains
elements (e.g., subgenera Delomegachile, Litomegachile
and Megachile s. str.) which exhibit facultative
sternotribic specialization by individual species on both
Compositae and Papilionoideae.

     As pointed out by Linsley and MacSwain (1957) in
their premiere article on sympatric speciation in bees,
such facultative specialization by generalists can
theoretically lead to allopatric and sympatric speciation
both, as long as the mating site is primarily associated
with flowers chosen for exploitation by the female.
Even in groups of bees in which there have been a great
deal of field studies completed, the site of mating is
seldom known with great certainty, since the successful
insemination event is of extremely short duration
(several seconds at most in many groups) except in
Nomadopsis, where the couple rides around in copula
for extended periods of time (even flying in tandem
between many flowers). In Dufourea, which I am
personally most familiar with, mating attempts are
frequently observed on flowers (perhaps hundreds in the
course of a day's observation) but in none of the
Dufourea species have I or my colleague Pat Lincoln
ever observed an unequivocably successful copulation
attempt. This fact coupled with the observation that
the rejection of the male is apparently because the
female is previously mated, and that in most species
the males also less frequently patrol nest site
aggregations and attempt to mate with returning
females, means that it is extremely difficult to unequi-
vocably state whether mating in one or another genus of
bees fulfills the preadaptation requirement for
sympatric speciation or not.

     Facultative host-specialization by a polylege
does not necessarily imply subsequent evolution of an
obligately host-specialized bee taxon. In fact, such
specialization events from presumed polylectic ancestors
are rather infrequent (Moldenke, 1979). Additionally,

there is an entire spectrum of possible diet types from theoretical random feeding (never realized in nature) to complete restriction to one particular species/ genus of plants. Certain bees, in fact, seem to be rather restricted to two completely unrelated plant genera; in most of these species, presumably individual bees go to both different plant genera and the population is not simply polymorphic in the expression of obligate host-specialization. _Dufourea vernalis_ is an example I have personally studied (with P. Lincoln, ms.) which carries mixed loads of _Gilia_ (_capitata_ and related species) and _Eschscholzia_ pollen in relatively equivalent amounts, regardless of the relative abundances and local distributions of the usual two host species; other genera are sometimes utilized in portions of its range where one or the other usual host plant is absent. Similar specialization upon two unrelated sympatric plant species is suspected or known in a small number of other cases (e.g., _Panurginus_ - Hydrophyllaceae+; _Anthidium_ - _Phacelia_ & _Lotus_; _Ashmeadiella timberlakei_ - _Lotus_ & _Phacelia_; _Andrena chlorogaster_ - _Ceanothus_ & _Lomatium/Sanicula_) and in the case of _A. chlorogaster_, _Anthidium_ spp. and probably some _Panurginus_ closely-related obligate feeding taxa restricted to either (but not both) of the plant genera utilized by the di-lege are known or suspected.

This type of "di-lecty" is distinct from the behavior exhibited by _Dufourea rhamni_ or _D. scintilla_ (Lincoln & Moldenke, ms.), which heavily emphasize and may actually require _Dendromecon_ and _Camissonia_ (respectively) but do in fact usually carry mixed pollen loads in their scopae; the identity of the additional pollen types varies widely from place to place. This foraging behavior pattern differs again from that of: a) generalist-feeding species which usually, but not invariably, utilize a particular dominant (perhaps) resource heavily in the presence of many other species of potential plant hosts; and b) generalists which utilize a particular plant host heavily only under circumstances where that particular host is disproportionately abundant; Hurd & Linsley (1975) have documented these patterns amongst the _Larrea_ bees of the southwestern United States.

The transition from generalist feeder, facultatively emphasizing different plants in different sites and at different stages of its temporal activity cycle (with no choice information presumably heritable or conditioned), to widespread obligate genus-specific monolectic feeder does not theoretically require the intermediacy of any of the former intermediate feeding strategies. The mechanism(s) of the shift from polylege $\longrightarrow$ specialist,

APPARENTLY EQUIVALENT	SOUTHWEST DESERTS	GREAT BASIN	GREAT PLAINS	EASTERN DECIDUOUS FORESTS	MEDITERRANEAN CALIFORNIA	MONTANE WESTERN STATES
siblings	38	15	14	21	23	32
non-siblings	31	14	11	12	12	13
TIME PHASE SHIFT						
siblings	16	0	1	0	4	2
non-siblings	3	1	1	1	2	0
CHANGE IN SIZE						
siblings	11	3	2	3	2	6
non-siblings	13	4	6	6	7	8
CHANGE IN HOST-CHOICE						
siblings	26	5	6	6	22	5
non-siblings	5	2	4	5	3	4
TOTALS						
siblings	91	23	24	31	52	46
non-siblings	53	21	21	23	25	25

TABLE 5. GENERAL DISTRIBUTION OF SYMPATRIC SPECIES CLUSTERS AND THEIR AXES OF DIFFERENTIATION.

which is the most frequent type of host choice shift
observed (Moldenke, 1979), is completely unknown and is
not explainable solely on the basis of the host-choice
patterns observed in sympatric sibling species, though
such analyses do implicate the existence of intermediate
feeding strategies at least in certain cases.

f) REGIONAL TRENDS IN CHARACTER DIFFERENTIATION:

        If one examines the data in Tables 1-4 from the
point of view of the geographical region in which the
different aspects of overlap occurs, the highest
instances are in the desert, mediterranean California
and the montane western United States respectively
(Table 5). However, since these regions support the
most diverse total bee faunas, this is not surprising.
When dealing with this information on a relative basis,
it must be noted that our knowledge of the bee fauna
is greatest for mediterranean California, followed by
the desert and clearly has the least resolution (in
terms of potential character displacement) in the
eastern United States. This means that fewer examples
of possible sympatry without any sort of behavioral
differentiation would be expected in the areas that
are better known, more examples of possible character
displacement having been noted. To the extent that
Table 5 verifies this bias, it points out in part the
unsuitability level of this type of data for the
analysis at hand.

        Approximately one-third of all the instances of
sympatric sibling species (Table 5) are encountered
in the arid southwestern deserts. In each of the
categories of sibling sympatric and con-subgeneric
sympatric species, the desert supports the highest
levels. Since the entries in the tables are not
strictly additive, it would be improper to compare
directly the proportions of closely-related sympatric
species in the different regions with the total number
of bee species recorded from each region. However,
by comparing these results in general to the total
bee species richness of the different regions of North
America, it is apparent that the desert southwest and
the montane western United States seem to support
somewhat more instances of sympatric congeneric
species than one would expect on the basis of total
bee species alone. This phenomenon is undoubtedly due
to unresolved differences in altitudinal preferences
amongst many of the species, which disqualifies a certain
proportion of these faunas as sympatric in reality.
The large proportion of montane western bees which are
placed in the categories signifying no known differences

between sympatric species, requires that the rest of
the column be under-represented and makes the dispro-
portionate number of size shifts more emphatic.   Such
size shifts in montane bees are quite probably correla-
ted with the aforementioned altitudinal or community
(sunny/shady) distinctions.

One interesting consistency of Table 5 is the
relative numbers of non-siblings and siblings demon-
strating distinct sympatric size divergences.   In all
cases the number of non-siblings outnumbers those of
siblings, implying perhaps that the short-term effects
of changing emergence dates or host-choice are easier
to effect than the complex physiological and develop-
mental shifts that might be inherent in changing body
size (for a determinate body growth plan).   However,
since the numbers are so small and our knowledge of the
actual instances of size divergence on a population
basis are so limited, I would personally interpret
these figures as only a possible indication that such
size changes are in fact difficult to attain evolu-
tionarily.

It is perhaps significant that in the mediterranean
California bee fauna the instances of host shifts are
more frequent than other types of displacement changes.
This trend is paralleled in all the other regions
(which remain less well studied) and perhaps indicates
that host switches are indeed the easiest form of
displacement to occur; it may possibly indicate that my
own interests lie along this subject, but the over-
whelming difference in numbers probably renders this an
unlikely possibility.   As I have taken pains to point
out repeatedly in this paper, our knowledge of all three
of these axes of possible divergence is very lacking,
and I doubt if it is any weaker in time and size than in
host divergence.   Any significant change in either the
time or the host-choice axis preadapts the bee for a
correlated change in the other axis; that the number of
host switch instances so far outnumbers those of time
phase shifts may indicate a certain inflexibility of
change in the cues used for emergence or may more likely
mean that the significant degree of time change is much
smaller than is possible to analyse with the present data.
(see Schoener, 1974, for comparison with other animals)

CONCLUSIONS:

Nearly all sibling bee species (broadly defined)
are basically allopatric.   There are instances of
sympatric siblings in all regions of North America,
most frequently in regions of high species diversity
and vice-versa.   Often when sympatric siblings do occur.

over broad geographic ranges that is, differentiation
is encountered in certain major characteristics.

Change in host occurs frequently from polylectic
to specialist; and infrequently between: 1) unrelated,
similar-appearing, synchronous blooming plant genera;
2) unrelated, dissimilar, synchronous-blooming plant
genera; and 3) between taxonomically related non-
synchronous plant genera.

Significant change in body size or flight
behavior probably alters energetic requirements
permitting character displacement relative to varying
resource availabilities. Such size changes occur most
frequently amongst presumed polylectic or "family-
specialized" species groups, which normally visit
floral resources of widely differing sizes and packagings,
and may in fact be associated with as yet undetermined
differential emphases in the preferred sizes of host
resource. Significant size differences amongst obligate
specialist feeders are not associated with floral size
per se, and most likely reflect energetic differences
in temporal activity patterns or resource spacing.
Significant size shifts are much more frequent between
sympatric relatively-unrelated equivalently specialized
congeners than between sympatric siblings.

Changes in resource utilization strategies by
competing social species are known in bumblebees and
presumed to occur within the social gradients evidenced
in the Halictinae.

Changes in temporal activities also occur between
sympatric siblings. Polyvoltine species apparently
shift to temporally limited univoltine taxa, with or
without the involvement of complete host specialization.
Phase shift occurs within short-lived species special-
ized on long-blooming resources, particularly between
bees specializing on the Compositae. Spring/summer
desert bloom switches occur in the western part of the
Sonoran Desert, especially on resource plants that
respond by flowering to both rainy seasons. Infrequent
examples of sibling species on the same resource plant
are known which are active during different time periods
of the day.

Many examples of sympatric sibling species are
known within which no obvious form of differentiation
is presently known. These are presumably due to
incomplete data, but the prevalence of polylege and
Compositae family-oligoleges within this category,
raises questions about the accepted assumptions of

"polylecty". Presumably localized populations of a
polylege often specialize differentially in the face of
different competitors and different host abundances;
if there is any possibility that larval food condi-
tioning plays a role in subsequent host-choice of adults,
such a mosaic of relatively stable feeding patterns in
polyleges would represent greater stability in many
pollination systems than currently realized. Experiments
on the mechanisms of host-allocation are especially
critical since oligolectic Compositae-feeding and
papilionaceous-feeding bee genera have frequently what
appears to be the most rapid speciation rates.

Sympatric speciation cannot be directly implicated
on the basis of present evidence, however, the existence
of sympatric sibling species (with or without differences
in some ecologically relevant character(s)) leaves the
process a distinct, but definitely infrequent, possibility.

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